Understanding evolution of plumages and other cyclic avian life-history phenomena

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UNDERSTANDING EVOLUTION OF PLUMAGES AND OTHER CYCLIC AVIAN LIFE-HISTORY PHENOMENA: ROLE FOR AN IMPROVED MOLT TERMINOLOGY

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Abstract. Birds show quite distinct changes in both external and internal appearance. An evolutionary interpretation of these cyclic life-history phenomena would benefit from a system of description aimed at mapping shared ancestries of arguably the ''easiest'' of traits: the molts and seasonal plumage changes. By 1959, Humphrey and Parkes had already provided the basis of such a system, but its development and application, especially with regard to the confusing first plumage cycle, by Howell et al. (2003), adds considerably to its power. I hope this leads to an upsurge of evolutionary studies of molt and plumage cycles that in turn provide the basis for analyses of other aspects of the flexible phenotype of birds. With such an increase, the study of molts and plumages could once again be at center stage of avian biology.

Key words: *annual cycles, life-cycle stages, molt, phenotype, phenotypic flexibility, seasonality.*

Entendiendo la Evolución de los Plumajes y Otros Fenómenos Cíclicos de las Historias de Vida de las Aves: El Papel de una Terminología Mejorada para la Muda

Resumen. Las aves muestran cambios bastante marcados en su apariencia externa e interna. Una interpretación evolutiva de estos fenómenos cíclicos de las historias de vida se beneficiaría de un sistema de descripción dirigido a mapear formas ancestrales compartidas de lo que se podría decir son los caracteres más ''fáciles'': las mudas y los cambios estacionales del plumaje. Hacia 1959, Humphrey y Parkes ya habían establecido la base de un sistema de este tipo, pero su desarrollo y aplicación, especialmente con respecto al confuso primer ciclo del plumaje, por parte de Howell et al. (2003) incrementan considerablemente su poder. Espero que esto lleve a un rápido incremento de estudios evolutivos de la muda y los ciclos del plumaje que a su vez provean la base para analizar otros aspectos del flexible fenotipo de las aves. Con un incremento tal, el estudio de la muda y el plumaje

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podría una vez más ocupar un lugar central en la ornitología.

The appearance of individual birds, with interesting exceptions, changes mainly through the growth of new feathers and their subsequent wear. Although it is the most eye-catching aspect, a changing plumage is only one of the many phenotypic changes shown by most birds in the course of a year (e.g., Murton and Westwood 1977, Gwinner 1986). A comprehensive understanding of the evolution of the highly variable plumages of birds therefore needs consideration of other cyclical aspects of avian life histories (Jacobs and Wingfield 2000), with due attention to the appropriate environmental context. In such an endeavor, the study of plumages seem an obvious place to start, but issues of shared ancestries and homologies provide a real obstacle for progress (Rohwer et al. 1992, Thompson and Leu 1994, Chu 1994, Jukema and Piersma 2000). The nomenclatural system designed by Humphrey and Parkes (1959; the H-P system) was ahead of its time and much underused, especially in the Old World. A revival of studies of the seasonally changing phenotype (e.g., Piersma and Drent 2003) now seems to be under way, so the critical development by Howell et al. (2003) of the H-P system aimed at mapping homologies comes at a good time. Being quite happy with the way in which the H-P system was developed and applied by Howell et al. (2003), I would like to widen the scope of their contribution and discuss how evolutionary studies of plumage variation can provide the basis for comprehensive assessments of the evolution of all cyclical aspects of avian life histories.

Sooner or later any in-depth study of birds has to come to grips with seasonal variation in phenotype, whether external or internal. In my own study on the life histories of long-distance-migrant shorebirds I have come to the realization that almost all phenotypic aspects are seasonally variable, and that this seasonal variability may tell us much about the selection pressures molding the birds' life histories (Piersma 2002, Piersma and Drent 2003). For example, some of the Bar-tailed Godwits (*Limosa lapponica*) staging in the Netherlands during northward migration show a supplemental molt of rusty-red contour feathers belonging to what was interpreted to be the alternate plumage (Piersma and Jukema 1993). That only individuals with relatively high body masses, complete alternate plumages, and a smaller likelihood of tapeworm infestation (Piersma et al. 2001) showed this supplemental molt, strongly suggested that the rusty-red plumage carried from spring until autumn signaled individual quality and was the outcome of sexual selection on both sexes. In addition, in Bar-tailed Godwits, and also in Ruffs (*Philomachus pugnax*), sexual selection pressure apparently has been so strong that the extravagant plumage of the breeding season in fact represents a third feather generation counting from the prebasic molt (Jukema and Piersma 2000). The bright new replacement feathers grown by Bar-tailed Godwits on spring staging areas (Piersma and Jukema 1993) count as a fourth.

A less conspicuous, but no less dramatic, seasonal change in avian phenotype was discovered in a study of preen-wax composition of Red Knots (*Calidris canutus*; Piersma, Dekker, and Sinninghe Damsté 1999). Before northward migration, or just after arrival on the High Arctic breeding grounds, individual Red Knots shift from producing a mix of well-known types of monoester waxes to a novel category of diester waxes (Sinninghe Damsté et al. 2000). We initially interpreted the production of diester waxes as a sexually selected quality signal visible to conspecifics, but subsequent analysis has demonstrated the shift to occur in almost all studied shorebird species, with the tightest correlation (with respect to sexes) with the timing of incubation rather than display and ornamental plumages (Reneerkens et al. 2002). Thus, the production of diester waxes during the breeding season may reflect natural selection (e.g., providing olfactory crypsis) rather than sexual selection.

A final example concerns the strongly variable size of the digestive tract of the Red Knot, a molluscivore that ingests hard-shelled prey whole, crushes the shells in a relatively heavy muscular gizzard and evacuates the shell fragments through the intestine (Battley and Piersma 2004). In the course of the year gizzard size doubles (smallest on the tundra breeding grounds, largest in midwinter), and these size changes can be interpreted as resulting from trade-offs between the capacity for digestive work, diet quality, energy requirements, and savings on maintenance and transport costs (van Gils et al. 2003). These changes may be the outcome of direct demand-supply processes, but strategic reductions in digestive organ size before long-distance flights (Piersma 1998, Piersma and Gill 1998, Piersma, Gudmundsson, and Lilliendahl 1999, Landys-Ciannelli et al. 2003) and gizzard size retention during a long-distance flight (Battley et al. 2000) strongly suggest that seasonal orchestration of organ size by endocrine pathways (Landys-Ciannelli et al. 2002) is also at play.

I now seem to have ventured very far from the issue of detecting homologies in the molts and plumages of birds. But here is my point: for a comprehensive understanding of the variable phenotype of organisms of all kinds, and especially in studies of the evolution of seasonally variable phenotypes, we need a seasonal ''template,'' a developmentally deep and basic phenotypic trait (or character, see Wagner 2001) that is easy to describe and well suited for intra- and interspecific comparisons. The seasonally changing plumages of birds provide us with such a trait (Wingfield and Jacobs 1999), but to date comparative descriptive studies of molts and plumages have been hampered by the lack of a robust and evolutionarily sensible terminology. In 1959, Humphrey and Parkes provided a good framework. I hope that Howell et al.'s alteration of the H-P system to facilitate the discovery of homologies, as well as their first categorization of molt strategies of bird families based on annual cycles (their table 1), will induce an upsurge of comparative studies of molt and plumage cycles. I am confident that ornithologists interested in other aspects of the flexible phenotype, and in the endocrine and neural orchestration of this flexibility, will be keen to build on these analyses. This would bring the study of molts and plumages back to the center stage of avian biology.

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